PCAS 21 (2018/2019)

Supervised Project

(ANTA604)

Fussy feeders or fallacy? Investigating the prevalence of prey preference in killer whales, globally and in the Southern Ocean.

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Word count: 9940 (excluding abstract and references)

Abstract (ca. 300 words):

Killer whales (*Orcinus orca*, Linnaeus 1758) are a cosmopolitan species, being found in all the world's oceans and most of its seas. There are currently ten ecotypes recognised globally and these distinct groups can be differentiated by variations in their morphology, societal structure, vocalisations, hunting techniques, genetic information, and prey preference. This study looked at the prevalence of prey preferences in killer whale populations, to understand whether their diets are genuinely as restrictive as they are perceived to be. Through analysing a high volume of literature, killer whales were found to predate on 159 different species. This data was compared to the perceived preferences of each ecotype to see how often the populations strayed from their preference. The Northern Hemisphere ecotypes were found to adhere more strictly to their preferred prey types; the Resident and North Atlantic Type I killer whales were found to not eat anything other than their preferred prey type. The Southern Hemisphere ecotypes displayed slightly more plasticity. The Gerlache (Type B, small) and Subantarctic ecotypes were also found to eat only their preferred prey, although the lack of data available for these isolated groups makes this observation less certain. Five of the remaining ecotypes, Transient, Offshore, Antarctic (Type A), Pack Ice (Type B, large), and Ross Sea (Type C), were found to display more generalist tendencies, feeding on a variety of prey, though still predominantly feeding on their preferred prey type. The conclusions drawn from this study was that, while there are some distinct differences between the ecotypes globally, prey preferences were often less restrictive than previously indicated. As they occupy the role as the top top predator in many of the world's oceans, understanding the prey each population eat, and how these may be impacted by climate change and future anthropogenic threats, is a crucial step in protecting this keystone species.

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ABSTRACT

Killer whales (*Orcinus orca*, Linnaeus 1758) are a cosmopolitan species, being found in all the world's oceans and most of its seas. There are currently ten ecotypes recognised globally and these distinct groups can be differentiated by variations in their morphology, societal structure, vocalisations, hunting techniques, genetic information, and prey preference. This study looked at the prevalence of prey preferences in killer whale populations, to understand whether their diets are genuinely as restrictive as they are perceived to be. Through analysing a high volume of literature, killer whales were found to predate on 159 different species. This data was compared to the perceived preferences of each ecotype to see how often the populations strayed from their preference. The Northern Hemisphere ecotypes were found to adhere more strictly to their preferred prey types; the Resident and North Atlantic Type I killer whales were found to not eat anything other than their preferred prey type. The Southern Hemisphere ecotypes displayed slightly more plasticity. The Gerlache (Type B, small) and Subantarctic ecotypes were also found to eat only their preferred prey, although the lack of data available for these isolated groups makes this observation less certain. Five of the remaining ecotypes, Transient, Offshore, Antarctic (Type A), Pack Ice (Type B, large), and Ross Sea (Type C), were found to display more generalist tendencies, feeding on a variety of prey, though still predominantly feeding on their preferred prey type. The conclusions drawn from this study was that, while there are some distinct differences between the ecotypes globally, prey preferences were often less restrictive than previously indicated. As they occupy the role as the top top predator in many of the world's oceans, understanding the prey each population eat, and how these may be impacted by climate change and future anthropogenic threats, is a crucial step in protecting this keystone species.

INTRODUCTION

Killer whales (*Orcinus orca*, Linnaeus 1758) are the largest member of the *Delphinidae* family and have been called the 'wolves of the sea' (Ferguson, Higdon & Westdal (2012). Other than humans, they are the most widely distributed mammal on earth, being found in all the oceans of the world and most of its seas (Ford, 2009). As a species, they occupy an extremely important role in many ecosystems as the top top predator, often regulating the abundances of other species (Guinet et al., 1992, Estes et al., 1998; Pitman & Durban, 2010). Currently only a single species of orca is recognised, though it is widely accepted that some of the populations found in regions around the world could potentially represent distinct species or subspecies (LeDuc, Robertson & Pitman, 2008; Morin et al., 2010). Some of these populations have been classed as ecotypes, of which ten are currently recognised. An ecotype is a distinct group of con-specific individuals which have adapted ecologically in response to environmental cues (Turrill, 1946). The term 'ecotype' was first described by Turesson (1922), when it was said to represent 'an ecological unit to cover the product arising as a result of the genotypical response of an ecospecies to a particular habitat'. That definition has since been extended to include individuals of the same species that have adopted similar ecological traits, regardless of their genealogical relationship to one another, and is often assigned based on ecological, not phylogenetic, differences (Turrill, 1946).

There are currently five ecotypes identified in each hemisphere; in the Northern Hemisphere there are the Resident, Transient, Offshore, North Atlantic Type I, and North Atlantic Type II killer whales, while in the Southern Hemisphere there are the Antarctic (Type A), Pack Ice (Type B, large), Gerlache (Type B, small), Ross Sea (Type C), and Subantarctic (Type D).

Figure 1. Overview of *Orcinus orca* ecotypes from the Northern and Southern Hemispheres (Image sourced from NOAA, 2016. Illustrations by Uko Gorter, text by Robert Pitman).

As a species, killer whales are generalist hunters, though many of the ecotypes show highly specialised behaviours, particularly in their prey preferences and cooperative hunting techniques (Ford, 2009; Pitman et al., 2011; Jourdain, Vongraven, Bisther & Karoliussen, 2017). Killer whale ecotypes can also be distinguished through differences in their morphology, social structure, vocalisations, and genetics (Pitman & Ensor, 2003; Pitman et al., 2011; Jourdain et al., 2017; Ford, 2018).

This study aimed to identify whether the perceived differences in the prey preferences of killer whale ecotypes are as stringent as previously indicated, or whether they are falsely perceived through observer bias or resulting from the assumption that the Southern Ocean ecotypes show the same dietary selectivity as those found in the Northern Hemisphere. Two questions that will be answered are:

(a) are killer whales universally always selective, or do they sometimes show dietary plasticity, e.g. as generalists versus specialists or through the prevalence of seasonal prey switching, and
(b) how probable is dietary specialisation in Antarctic killer whales?

This report will also examine the ecological significance of having a strong prey preference, including advantages and disadvantages, and any conservation implications. The multitude of challenges and limitations found while analysing the data and any criticisms identified while reviewing the literature will also be discussed.

To understand the extent of prey preferences in killer whale populations, a meta-analysis was carried out that looked at a range of sources, including peer-reviewed journal articles, video footage, and news articles. The data gathered through this study was then compared with the perceived preferences of each ecotype to identify how often members of an ecotype eat prey that lies outside of their perceived preferred prey type. The perceived preferences that form the baseline in this study are based on references in popular literature, particularly the expanse of work by Pitman and Ford.

METHODOLOGY

This study involved examining peer reviewed journal articles to identify what prey killer whales were eating globally. Other sources, such as videos uploaded to YouTube and Facebook, as well as news articles, were included in the analysis to provide a broader scope to accurately examine the killer whale diet. As the sources were reviewed, any time the author stated that a predation event occurred, or a prey item was found in the stomach of a stranded or hunted orca, the information was collated in a Microsoft Excel spreadsheet (Appendix A). The information gathered from the resources included:

i) type of prey
ii) location
iii) ecotype or population involved
iv) source where the information was read
v) original paper cited by the authors (if available)
vi) any additional details (if available)

This data was then analysed to identify whether the observed prey for each ecotype aligned with their perceived prey preference.

Prey types were separated into seven classes: cetaceans, pinnipeds, bony fish, seabirds, elasmobranchs, cephalopods, and ‘other’. For accuracy, fish were separated into elasmobranchs, which includes all sharks and rays, and bony fish, which includes all other bony and cartilaginous fish species. This distinction has been made due to the very different hunting techniques required for these two groups and the distinct specialisation often observed within elasmobranch hunters. The ‘other’ class included species which did not align perfectly in any of the other classes, i.e. turtles, ungulates, crabs, and river otters.

Some of the literature used prey descriptions, such as ‘marine mammal’, ‘baleen whale’, or ‘fish’, which did not align with the overall classification methodology. The decision was made to keep this data in the overall data set, because, while they failed to identify the exact species, these reports still aided in highlighting when some ecotypes stray from their preferred type of prey.

RESULTS

In the literature reviewed for this study killer whales were recorded eating 178 different prey types, of which 159 were identified to the species or genus level (Table 1). The species identified as prey include 61 marine mammals, comprising of 35 cetaceans, 24 pinnipeds, and two species of otter. The study also identified 18 seabird species, 47 fish species and 21 elasmobranchs (Table 1). Overall, this data highlighted the vast breadth of prey that killer whales, as a species, consume. Analysis highlighted some unusual findings, such as the presence of three ungulate (hooved) land mammals in killer whale diet, which were deer, moose, and pig in the eastern North Pacific region, all of which are assumed to have been scavenged or hunted while swimming between islands.

Table 1. Total prey types gathered through analysis of literature. Prey types include broader classifications such as marine mammals or fish. Prey species represent those which are identified to the species or genus level.

Prey types	178
Prey species	159
Marine mammals	61
Cetaceans	37
Pinnipeds	24
Seabirds	18
Fish	49
Elasmobranchs	21
Cephalopods	2
Other	8

When the data was compared to the perceived prey preferences of each ecotype it was found that only four of the ten ecotypes strictly predate on only their preferred prey type (Table 2) (Figure 12). These ecotypes were the Resident and North Atlantic Type I killer whales in the Northern Hemisphere and the Gerlache and Subantarctic killer whales in the Southern Hemisphere, although the limited data available for the two Southern Hemisphere ecotypes could be an influential factor in this finding. The predation habits of the Gerlache killer whale only featured in four reports, while the predation habits of Subantarctic killer whales were even more rare, only appearing in two. This potentially contributed to the lack of evidence that these groups stray from their preference and aids in highlighting the significant limitation that exists with sampling bias in this type of study. Resident killer whales appeared in 35 different reports, the third highest out of the ecotypes, and were not reported to have eaten anything other than fish or squid, meaning that this group could be considered the most restrictive feeder out of all the ecotypes globally. An important consideration when analysing the data was the number of reports of each prey type, as this provides insight into how often the group may stray from their perceived preference. The results for each ecotype have been broken down individually.

Table 2. Summary of the perceived preference for each ecotype and the types of prey that was identified as part of their diet. Only the Resident, North Atlantic Type I, Gerlache, and Subantarctic killer whales were found to have not strayed from their preferred diet in this study.

	Preferred diet	**Identified diet**		
Transient	Cetaceans Pinnipeds	Cetaceans Pinnipeds	Seabirds Squid	Other
Resident	Fish Squid	Fish Squid		
Offshore	Fish	Fish Elasmobranchs	Seabirds	
North Atlantic Type I	Fish Pinnipeds	Fish Pinnipeds		
North Atlantic Type II	Cetaceans	Cetaceans Fish		
Type A Antarctic	Cetaceans Pinnipeds	Cetaceans Pinnipeds	Fish Seabirds	Elasmobranchs
Type B (big) Pack ice	Pinnipeds	Pinnipeds Cetaceans	Fish Seabirds	
Type B (small) Gerlache	Penguins	Penguins		
Type C Ross Sea	Fish	Fish Cetaceans	Seabirds	
Type D Subantarctic	Unknown	Fish		

RESIDENT

The perceived prey preferences for this ecotype are fish and squid, with some populations being perceived to feed entirely on salmon. Resident killer whales were found to predate on only fish and squid, adhering most tightly to the perceived preference for the ecotype (Figure 2). There were 31 records which involved Resident killer whales and they were found to eat 19 different types of prey, including six species of salmon. These reports originated from Vancouver Island in the eastern North Pacific and extended across the Bering Sea to the Kamchatka Coast in northern Russia. Few reports mention the season of the observations; however, it is thought that this group eat the same prey year-round, relying heavily on one species in particular, chinook salmon (*Oncorhynchus tshawytscha*, Walbaum 1792), which was identified as a prey species on seven occasions (Figure 2). Other species of salmon that were identified as less significant prey included chum (*O. keta*, Walbaum 1792), coho (*O. kisutch*, Walbaum 1792), sockeye (*O. nerka*, Walbaum 1792), and pink (*O. gorbuscha*, Walbaum 1792). Such a strict prey preference can have radiating effects on population dynamics, particularly when the prey species is threatened. These implications will be discussed further in the following section

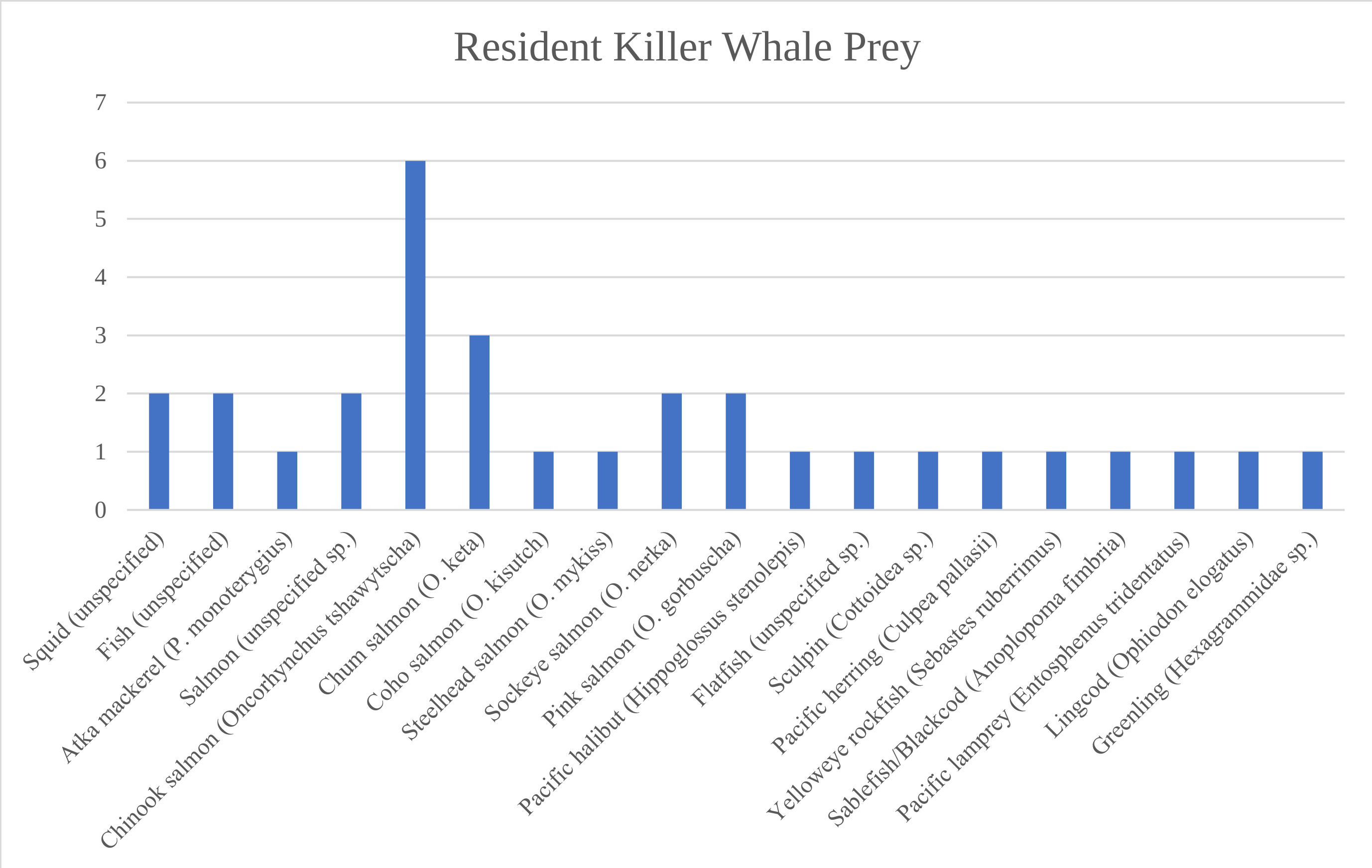

Figure 2. Graph highlighting the types of prey that the Resident ecotype has been recorded eating. This group did not stray from their preferred prey of fish and squid. This group showed a strong preference for salmon, which represented seven of the 19 prey types identified.

TRANSIENT (BIGG'S)

The perceived prey preference for Transient killer whales is marine mammals. Transient killer whales were found to predate on a wide variety of species, including cetaceans, pinnipeds, seabirds, squid, and ungulates (Figure 3). Reports identified 30 different prey types, with 26 of those being identified to the species level. This group featured most often in the literature, with 69 reports discussing predation events that involved Transient killer whales. The most common prey type was harbour seals (*Phoca vitulina*, Linnaeus 1758), which featured 11 times. There were five predation events involving grey whales (*Eschrichtius robustus*, Lilljeborg 1861), and four events each involving minke whales (*Balaenoptera acutorostrata*, Lacépède 1804), Dall's porpoises (*Phocoenoides dalli*, True 1885), Steller sea lions (*Eumetopias jubatus*, Schreber 1776), and unidentified seabirds (Figure 3). Interestingly, as this group lives sympatrically with the Resident ecotype and has much of the same prey available, neither group were seen to predate on any of the same species, apart from squid. Their preferred prey type was found to be the most dominant from the 30 identified in the literature, indicating that, while this group has some generalist tendencies, they still predominantly feed on their preferred prey type.

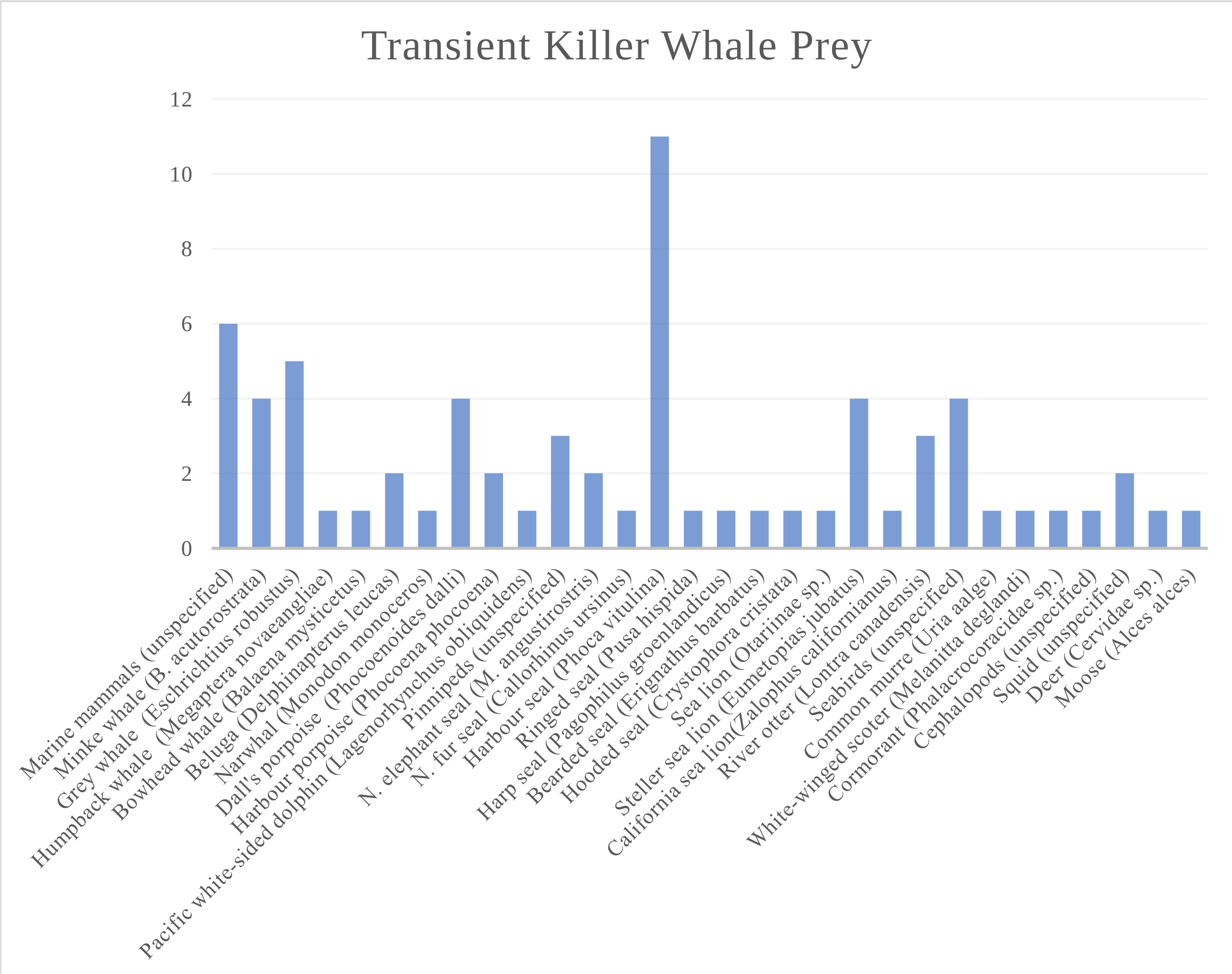

Figure 3. Graph highlighting the types of prey that the Transient ecotype predate on. This group featured most heavily in the literature and was found to eat a wide variety of prey, some of which lay outside their marine mammal preference. Harbour seals occurred most commonly, represented by 11 separate reports. Grey whales, minke whales, Dall's porpoises and Steller sea lions were the next most frequent prey species. They were also found to predate on river otters (*Lontra canadensis*, Schreber 1777), cephalopods, ungulates, and a range of seabirds.

OFFSHORE

The perceived prey preference for the Offshore ecotype is <u>fish</u>. Offshore killer whales were found to predate on fish, sharks, and turtles (Figure 4). There were ten reports of predation events involving Offshore killer whales and they were found to eat seven different types of prey. Due to the limited volume of literature involving this group, definitive conclusions are difficult to draw. This could be related to the less accessible range of the group, compared to the Resident and Transient ecotypes which live in the same region but nearer shore. Interestingly, one report stated that an unspecified crab species was found in the stomach of a stranded Offshore killer whale (Barrett-Lennard & Heise, 2006). It was unclear, however, if it was a result of predation or a secondary prey item (i.e. the prey of one of the other species also found in the orca's stomach). Fish was found to be the dominant prey type from the seven identified in the literature. While they occasionally stray to more unusual prey, such as a leatherback turtle (*Dermochelys coriacea*, Vandelli 1761) and a Pacific sleeper shark (*Somniosus pacificus*, Bigelow & Schroeder 1944), they were found to predominantly feed on their preferred prey type.

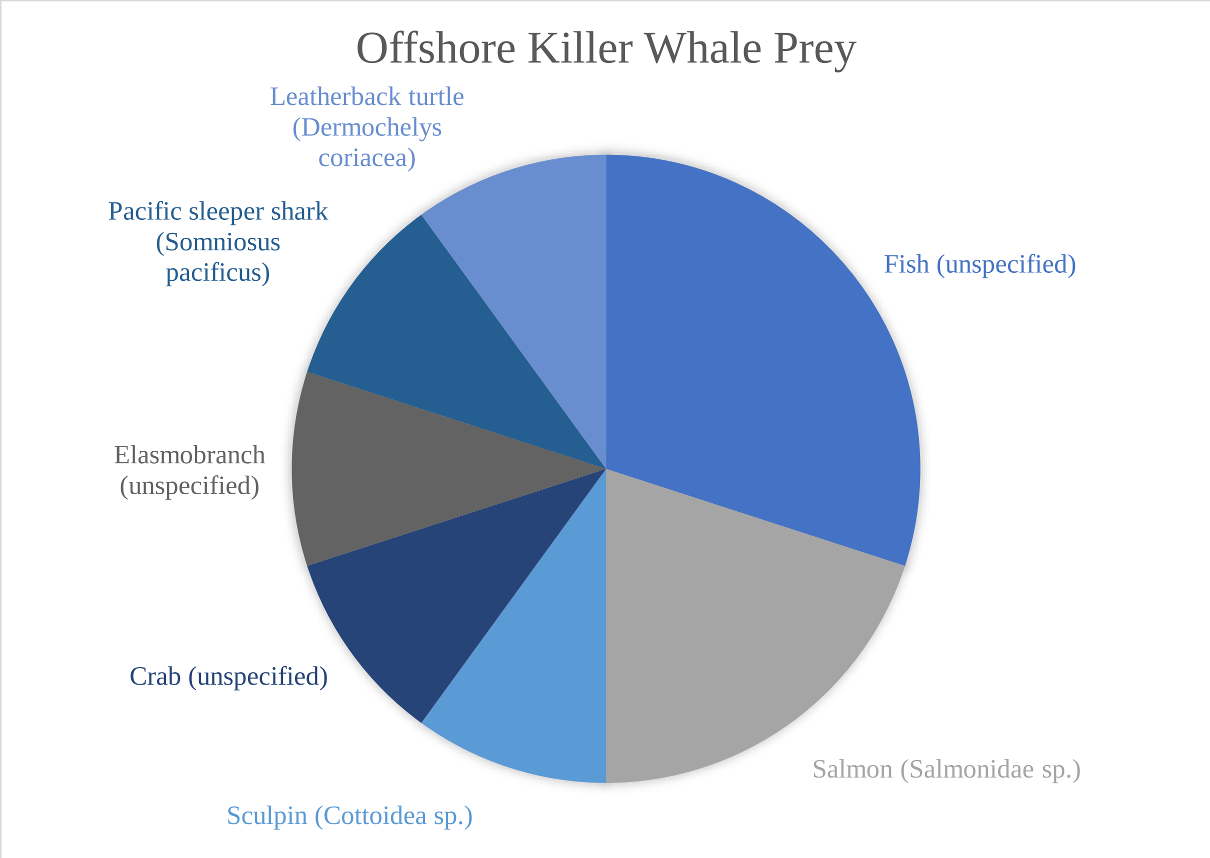

Figure 4. Graph highlighting the type of prey that the Offshore ecotype predate upon. This ecotype showed a marked reliance on fish, their preferred prey type, but did occasionally exploit other types of prey.

NORTH ATLANTIC TYPE I

North Atlantic Type I killer whales is considered to be a generalist, feeding on fish, pinnipeds, and elasmobranchs. The literature recorded their predation on pinnipeds and fish (Figure 5). There were 12 records which involved this group and they were found to eat eight different types of prey, five of which were identified to the species level. Besides the Residents, this group was the only other Northern Hemisphere ecotype which did not stray from its perceived prey preference. While this group is perceived to be a generalist, much of the literature reviewed in this study indicated a heavy reliance on fish. Herring (*Clupea harengus*, Linnaeus 1758) was the species most commonly eaten by this group, followed closely by grey seals (*Halichoerus grypus*, Fabricius 1791) and unspecified fish. A challenge faced with accurately identifying the prey species of both the North Atlantic ecotypes was an apparent confusion over the population identities. Some publications agreed that there are North Atlantic Type I and Type II, however, two additional reports were found that separated the population into three distinct groups, A, B and C (Wellard et al., 2016; Samarra et al., 2018). This meant that many of the species identified as prey for these three groups could not be included in the analysis due to it being unclear which ecotype is being referred to.

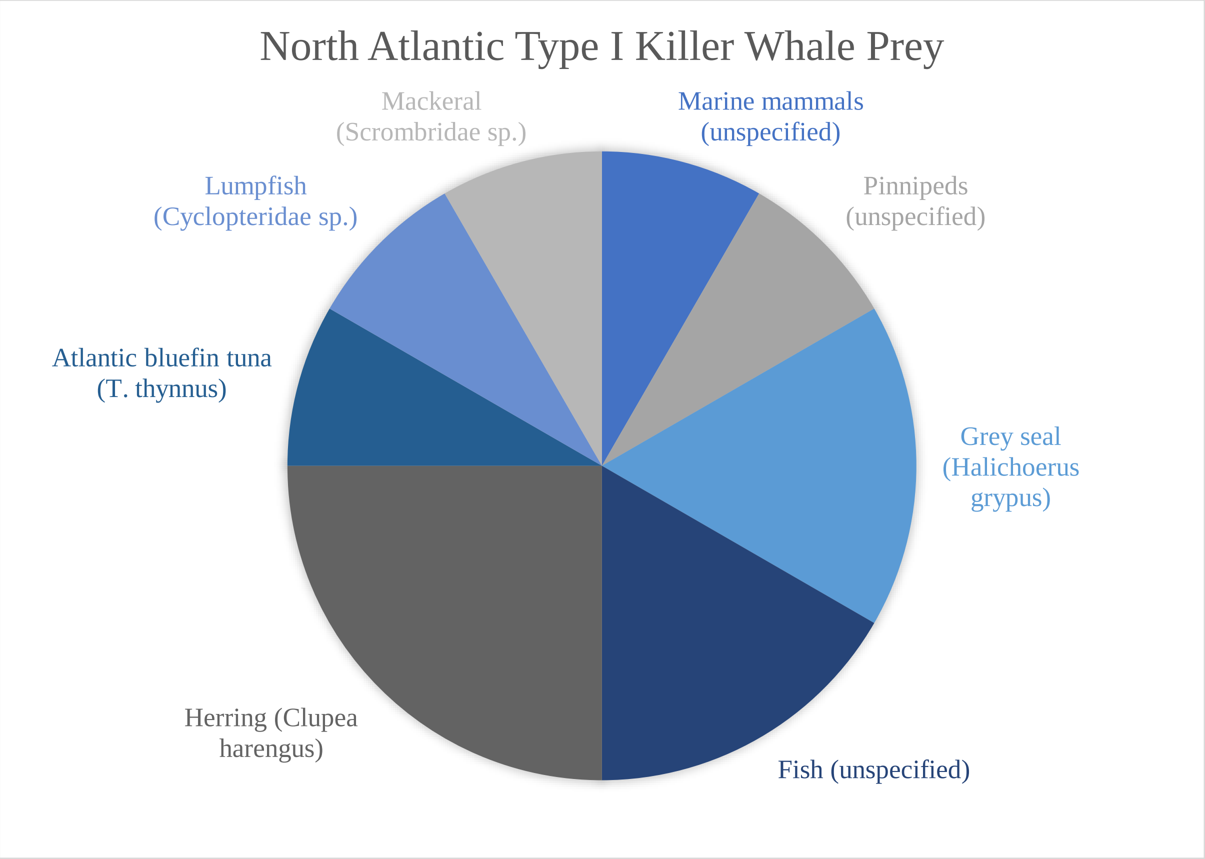

Figure 5. Graph highlighting the type of prey that the North Atlantic Type I ecotype predate upon. This ecotype is considered to be a generalist population and for that reason, while the predated on a wide variety of prey, this was not considered to be unusal for the group. This ecotype fed mostly on fish, which made up more than two-thirds of their diet. The remainder was marine mammals.

NORTH ATLANTIC TYPE II

The perceived prey preference for this ecotype is cetaceans, while this study found that North Atlantic Type II killer whales predated on cetaceans and fish (Figure 6). There were five records which involved this group, and these reported four types of prey. The only accurately identified species for this ecotype was the harbour porpoise (*Phocoena phocoena*, Linnaeus 1758), which was represented by just one record. A challenge highlighted by this group was the lack of accurate definition surrounding the prey species. A report by de Bruyn, Tosh and Terauds (2012) stated that 'baleen whales' had been identified as a prey type for this group in the North Atlantic region through stomach contents analysis, but the exact species was not identified. Literature also identified fish (unspecified species) as prey for this group, indicating that they do stray from their cetacean preference on occasion (Figure 6).

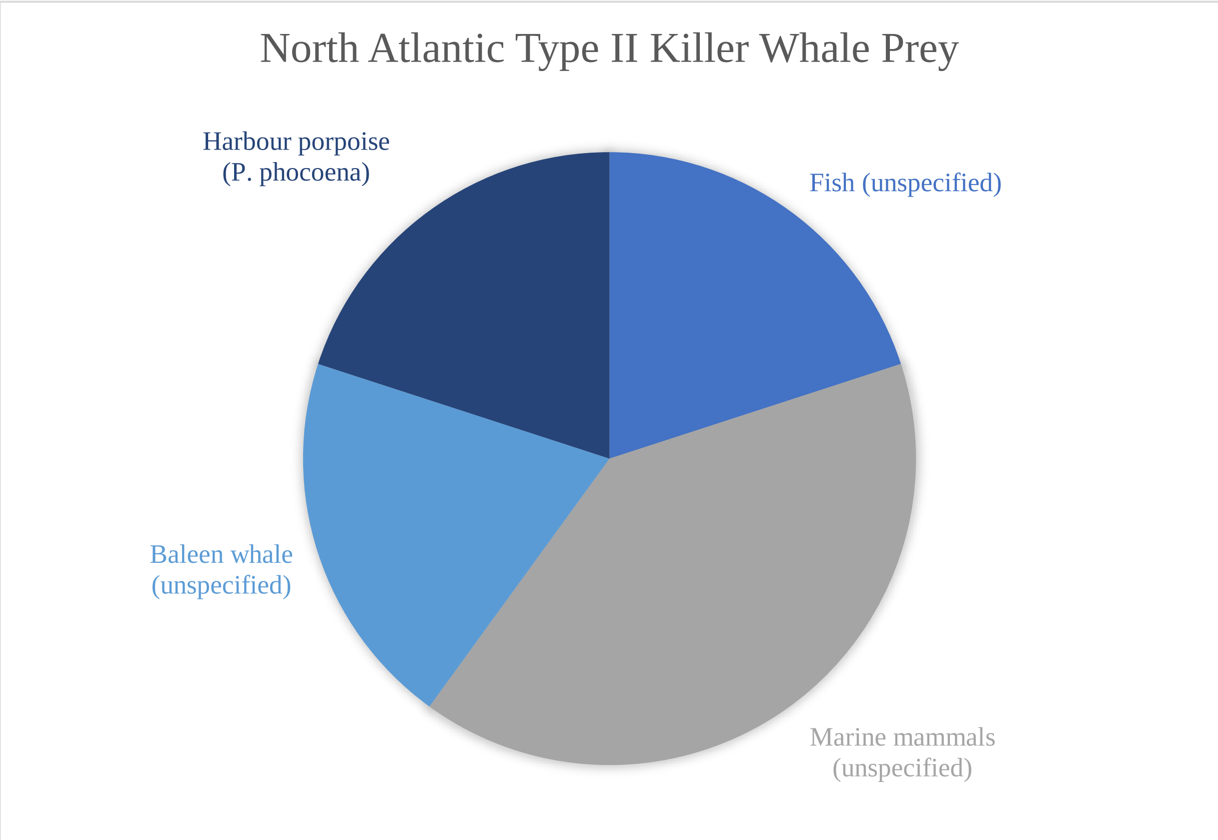

Figure 6. Graph highlighting the type of prey that the North Atlantic Type II ecotype predates on. This ecotype is percieved to prefer marine mammals. Marine mammals remained the dominant prey type, however, the literature found that fish also feautured, representing almost a quarter of all predation reports.

ANTARCTIC (TYPE A)

The perceived prey preferences for this group are <u>cetaceans and pinnipeds</u>. Reports examined during this study found that Antarctic killer whales predate on a wide variety of species, straying considerably from their marine mammal preference (Figure 7). Other than cetaceans and pinnipeds, Antarctic killer whales were also seen predating on seabirds, fish, squid, elasmobranchs, and turtles (Figure 7). This group appeared in the literature 46 times and were found to eat 24 different prey types. The locations of these reports ranged from the ice-free water of Antarctica up to the more temperate ocean surrounding Australia, New Zealand, and South America. Due to the differences in prey availability in these different regions, it appeared that the preference of this group is highly seasonal. Unspecified fish represented a significant portion of the reports, being mentioned as prey seven times. Other significant prey were southern elephant seals (*Mirounga leonina*, Linnaeus 1758), which featured four times, and minke whales (*B. bonaerensis*, Burmeister 1867), which featured three times. As previously highlighted in the North Atlantic Type II section, the lack of precise identification of the type of fish which was eaten as prey is a limitation of this analysis. Their preferred prey types did feature in their diet, however, not to the extent that would be expected. Fish and seabirds also featured considerably, indicating a much more generalist diet than some of the literature indicated.

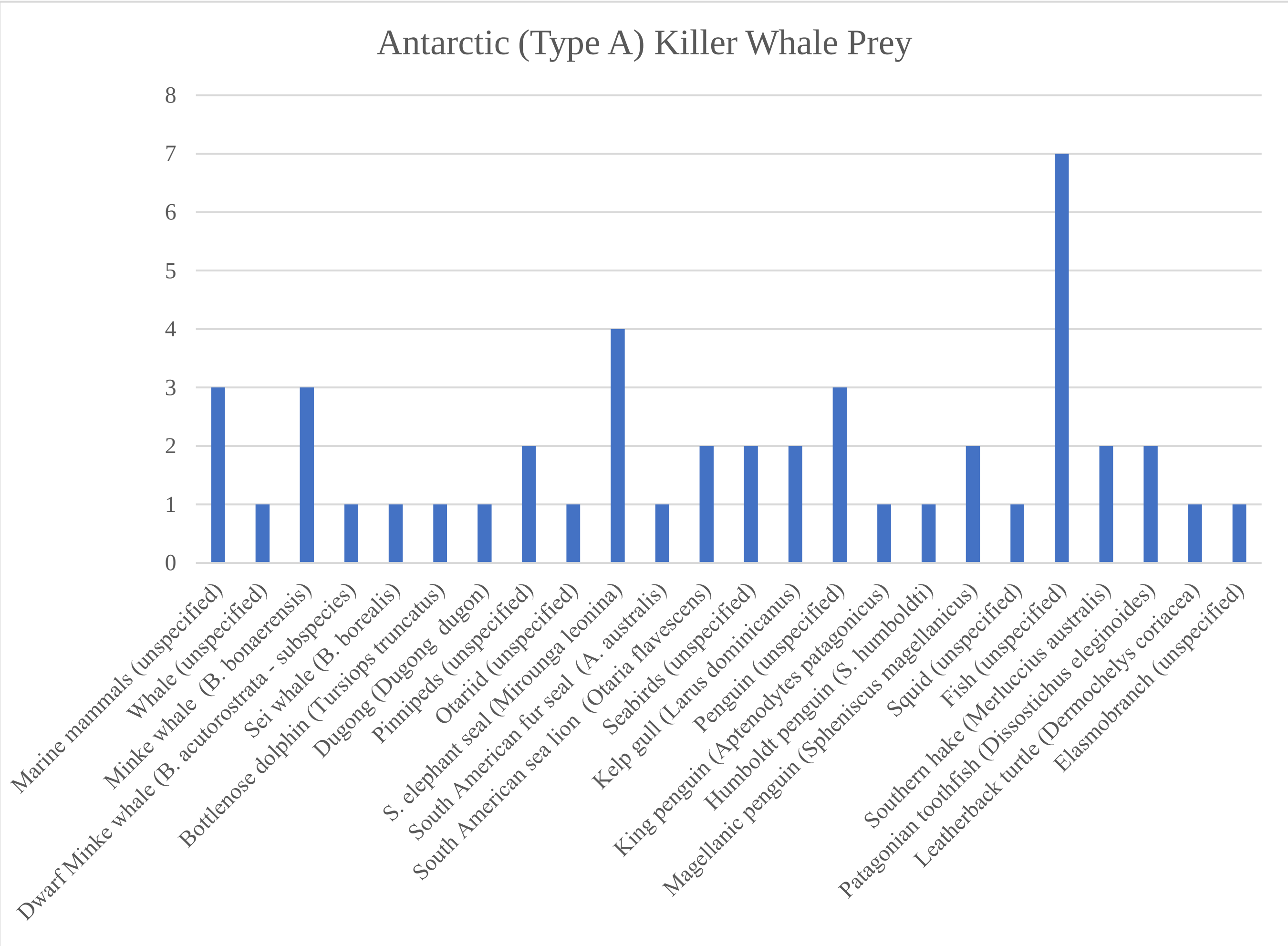

Figure 7. Graph highlighting the types of prey that the Antarctic (Type A) ecotype predates on. This group featured most heavily out of its Southern Hemisphere counterparts and was found to eat a wide variety of prey. The perceived preference for this ecotype is marine mammals, which they predated on 21 times in total. Fish predation events were reported on 14 occasions. They were also found to predate on six types of seabird. Southern elephant seal and minke whale were the marine mammals that occurred most frequently.

PACK ICE (TYPE B, LARGE)

The perceived prey preference for this group is <u>pinnipeds.</u> Pack Ice killer whales were found to predate on cetaceans, pinnipeds, sea birds, and fish (Figure 8). There were 42 records which involved this group and they were found to eat 17 different types of prey. The main species that were predated on by this ecotype were crabeater seals (*Lobodon carcinophaga*, Hombron & Jacquinot 1842), humpback whales (*Megaptera novaeangliae*, Borowski 1781), southern elephant seals, and leopard seals (*Hydrurga leptonyx*, Blainville 1820). All the reports involving this ecotype originated from the Southern Ocean and Subantarctic Islands, and while some reports indicate potential migratory behaviour to more temperate waters, the feeding habits on these migrations have not been observed. Their preferred pinniped prey was found to feature heavily in the reports involving this group. This ecotype has the capability to hunt a wide variety of prey, including large whales and small penguins, as well as depredating Patagonian toothfish (*Dissostichus eleginoides*, Smitt 1898) off longlines. This type shows some generalist tendencies, however, they still predominantly feed on their preferred pinniped prey (Figure 8).

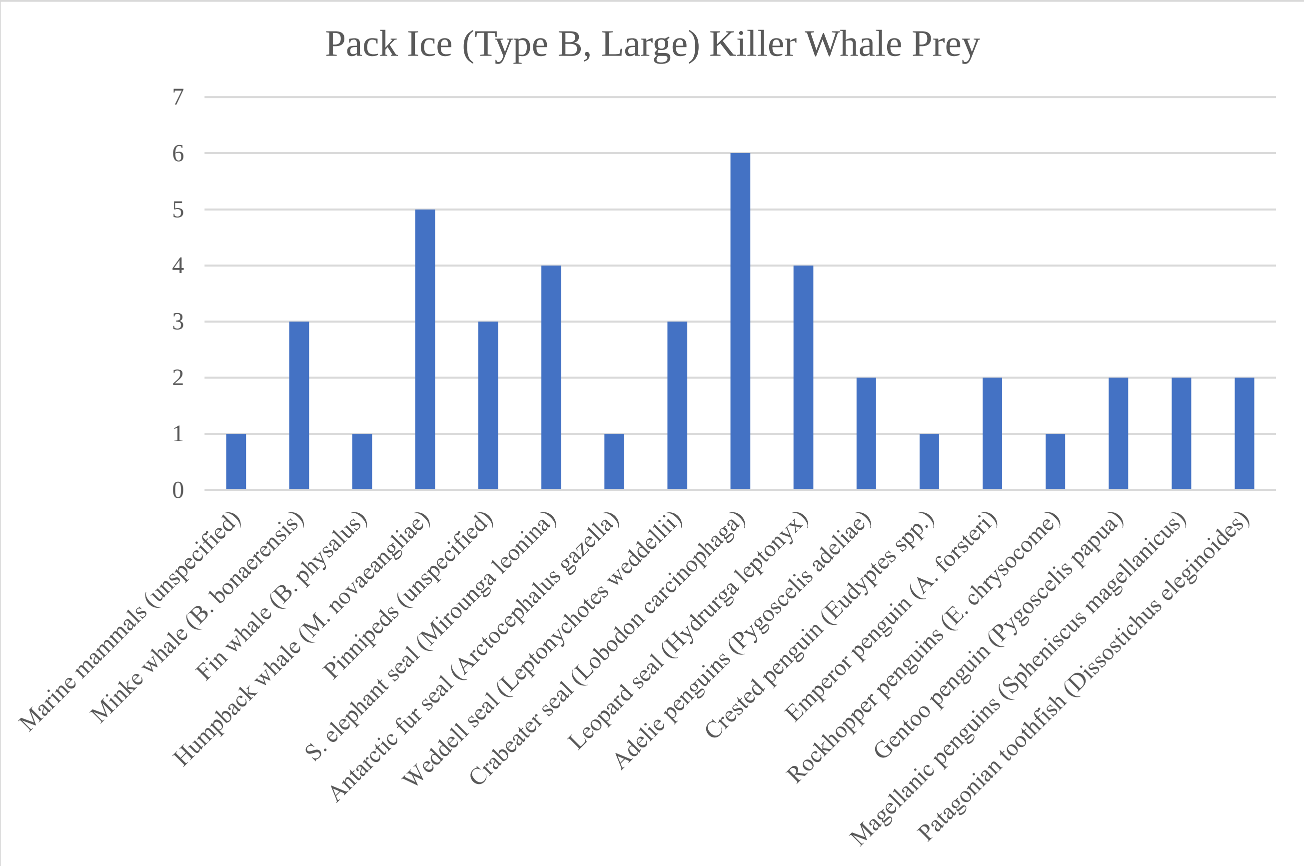

Figure 8. Graph highlighting the types of prey that the Pack Ice (Type B, large) ecotype predates on. This group was found to predate on a range of prey, diverting on occasion from their pinniped preference. Crabeater seals were the most common prey for this group, followed closely by humpback whales, southern elephant seals and leopard seals.

GERLACHE (TYPE B, SMALL)

The perceived prey preference for Gerlache killer whales is penguins. They were found to predate only on penguins and was one of the two Southern Hemisphere ecotypes, along with the Subantarctic killer whales, which were witnessed predating on nothing but their preferred prey (Figure 9). There were only four records identified which involved this group and they were found to eat two penguin species, chinstrap (*Pygoscelis antarcticus*, Forster 1781) and gentoo (*P. papua*, Forster 1781). All the reports originated from the Gerlache Strait on the Antarctic Peninsula. The limited number of reports brings some uncertainty into the conclusion that this group never strays from their preference and illustrates the possible limitation of sampling bias.

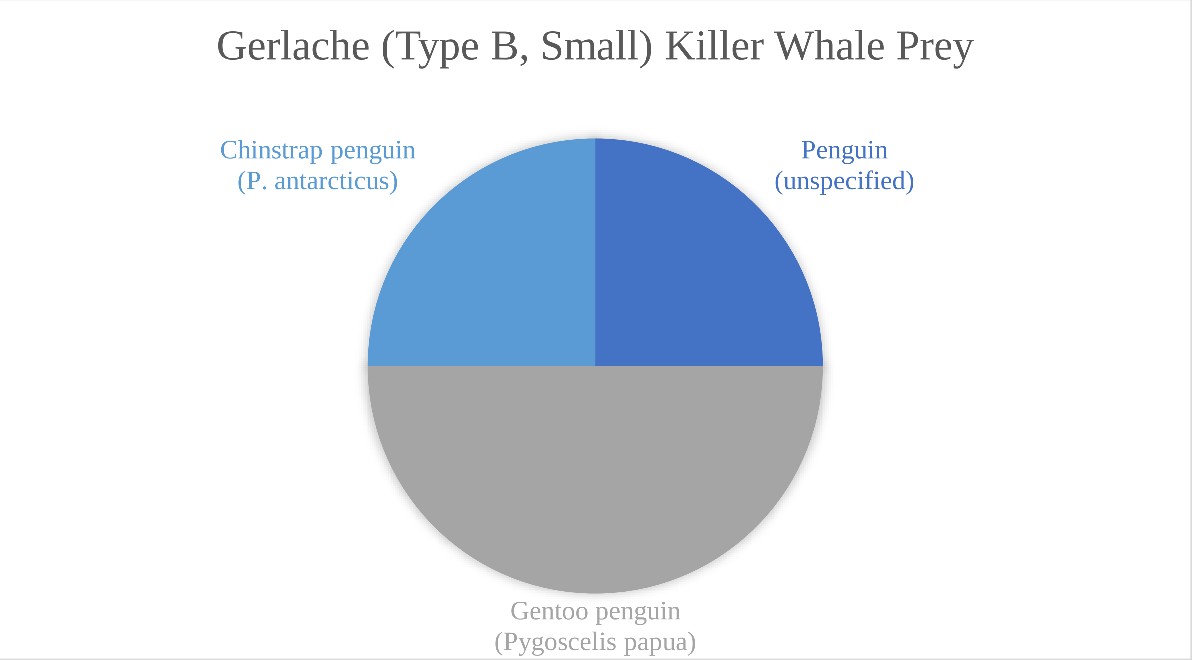

Figure 9. Graph highlighting the types of prey that the Gerlache (Type B, small) ecotype predates on. This group only feautured four times in the literature and were found to only predate on penguins.

ROSS SEA (TYPE C)

The perceived preferred prey for this group is fish. Ross Sea killer whales were found to predate on seabirds, fish, and cetaceans (Figure 10). There were 11 records which involved this group and they were found to eat seven different types of prey. The group which featured most frequently was fish, with three reports identifying Antarctic toothfish (*D. mawsoni*, Norman 1937) as a significant part of their diet. Reports indicate that this group also travels to temperate waters of the Southern Hemisphere (Eisert et al., 2015), though their predation habits during these migrations was not commented on. The reliability of some of these reports is somewhat questionable, where the authors state that harassment of prey, such as humpback whales, was observed but predation could not be confirmed. The potential speciation of the Southern Hemisphere ecotypes, which was suggested by Berzin and Vladimirov (1983), also highlights another challenge. As they separated the Southern Hemisphere groups into two species, *O. orca* and *O. glacialis*, there is some disagreement around which group they were looking at when reporting on stomach contents. Due to the yellow colouration and small size, it is believed *O. glacialis* represents the group known today as Ross Sea killer whales. Stomach content analysis found 0.4% to contain marine mammal, 1.1% to contain squid and 98.5% to contain fish (Berzin & Vladimirov, 1983). This is discussed further in the limitations section of the report.

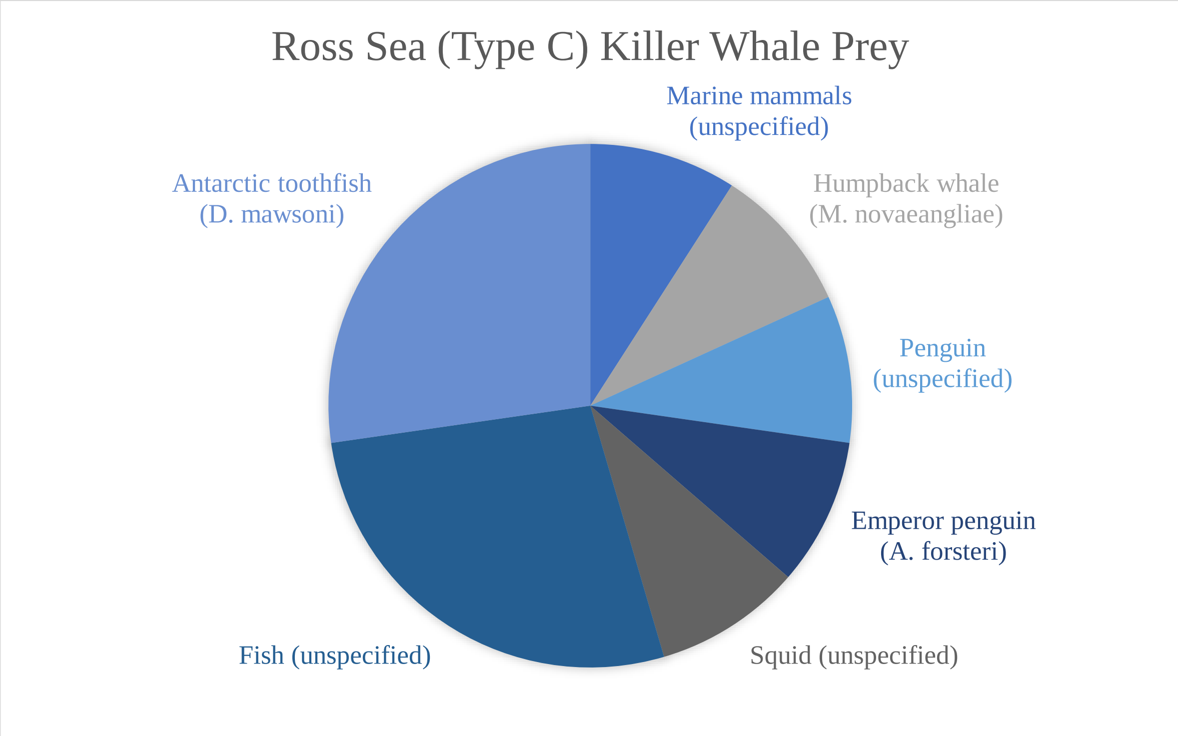

Figure 10. Graph highlighting the types of prey that the Ross Sea (Type C) ecotype predate on. The preferred prey of this ecotype is fish and this was confirmed in the literature. This group was also found to predate on some species which lay outside their preference, though the accuracy of that data was uncertain.

SUBANTARCTIC (TYPE D)

Subantarctic killer whale's preferred prey type is currently unknown, although it is suspected to be fish. They only appeared in the literature twice, with both records highlighting depredation of Patagonian toothfish from longlines in the Subantarctic (Figure 11). Similar to the data available for the Gerlache ecotype, the limited number of reports makes drawing the conclusion that this group eats nothing but fish uncertain.

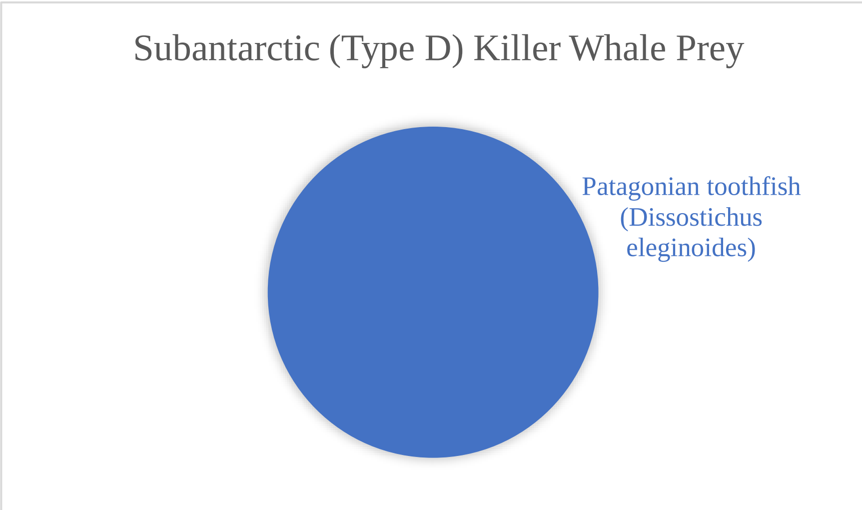

Figure 11. Graph highlighting the type of prey that the Subantarctic (Type D) ecotype predates on. There were only two reports which discussed predation events for this ecotype and both spoke of the same species, Patagonian toothfish.

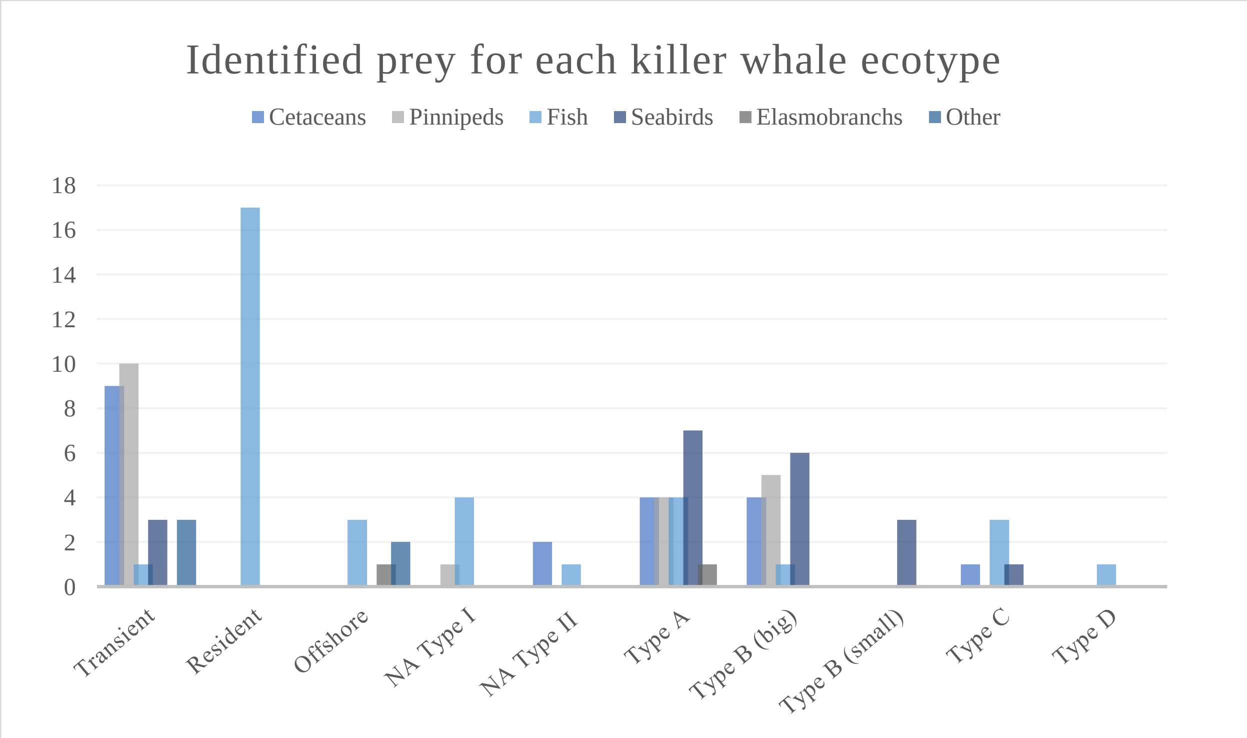

Figure 12. Summary of the types of prey each ecotype were reported to have eaten.

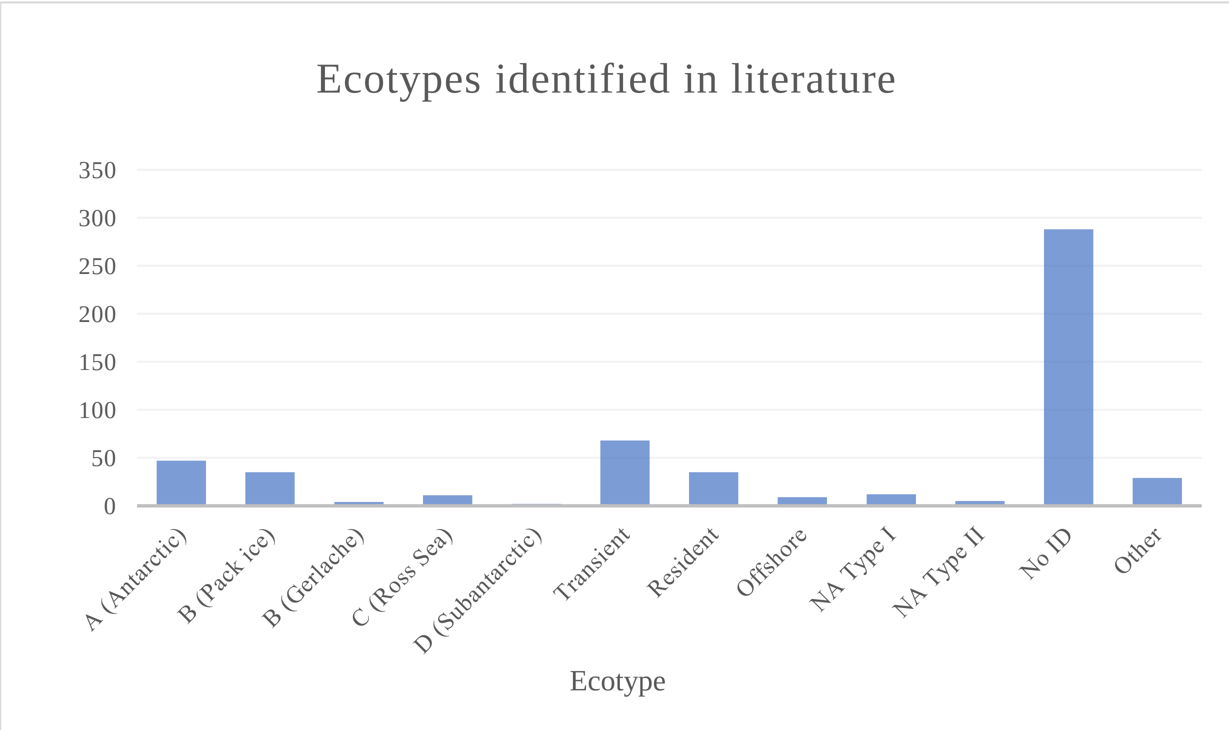

Figure 13. Graph highlighting the number of reports that failed to identify the ecotype or population responsible for the predation event. Transient killer whales were identified most often, followed by Antarctic, Pack Ice and Resident. 'Other' included North Atlantic Type A, B and C classifications that some literature used, as well as distinct populations, such as the New Zealand's population, which has shown to be different from any other Southern Hemisphere ecotype.

Out of the 178-prey types identified, 61 were not associated with an identified ecotype (Figure 13). This meant that, while the data helped to demonstrate the vast range of prey consumed by killer whales as a species, many of the reports failed to provide insight into whether these predation events were out of the expected range for a particular ecotype. Some of the species that were identified as killer whale prey, without identifying the ecotype responsible, included blue whale (*B. musculus*, Linnaeus 1758), sperm whale (*Physeter macrocephalus*, Linnaeus 1758), Baird's beaked whale (*Berardius bairdii*, Stejneger 1883), three species of fur seal (*Arctocephalus forsteri*, Lesson 1828; *A. tropicalis*, Gray 1872; *A. pusillus*, Schreber 1775), and five species of tuna (*Katsuwonus pelamis*, Linnaeus 1758; *Thunnus albacares*, Bonnaterre 1788; *T. obesus* Lowe 1839; *T. alalonga*, Bonnaterre 1788; *T. maccoyii*, Castelnau 1872) (Table 3).

Table 3. Table listing the species that were identified as prey for killer whales without the ecotype identification being available. These species aided in highlighting the vast breadth of species which killer whales consume but were unable to be used in the ecotype prey preference analysis.

Ecotype not identified	
Blue whale (*Balaenoptera musculus*)	Octopus (unspecified)
Sperm whale (*Physeter macrocephalus*)	Pacific salmon (*Oncorhynchus spp.)*
Pygmy sperm whale (*Kogia breviceps*)	Australian salmon (*Arripis trutta*)
Dwarf sperm whale (*K. sima*)	Halibut (*Hippoglossus spp.*)
Bryde's whale (*B. brydeii*)	Arrowtooth flounder (*Atheresthes stomas*)
Short-finned pilot whale (*Globicephala macrorhynchus*)	Swordfish (*Xiphias gladius*)
N. Right whale (*Eubalaena spp.*)	Tuna (unspecified)
S. Right whale (*E. australis*)	Skipjack tuna (*Katsuwonus pelamis*)
Pygmy Right whale (*Caperea marginata*)	Yellowfin tuna (*Thunnus albacares*)
Finless porpoise (*Neophocaena phocaenoides*)	Bigeye tuna (*T. obesus*)
Killer whale (*O. orca*)	Albacore tuna (*T. alalunga)*
False killer whale (*Pseudorca crassidens*)	Southern bluefin tuna (*T. maccoyii*)
Common dolphin (*Delphinus spp.*)	Indo-Pacific sailfish (*Istiophorus platypterus*)
Striped dolphin (*Stenella coeruleoalba*)	Bluenose warehou (*Seriolella brama*)
Pantropical spotted dolphin (*S. attenuata*)	Sunfish (*Mola mola*)
Beaked whales (unspecified)	Southern sunfish (*M. alexandrini*)
Baird's beaked whale (*Berardius bairdii*)	Giant trevally (*Caranx ignobilis*)
Cuvier's beaked whale (*Ziphius cavirostris*)	Deep sea/blue eye trevalla (*Hyperoglyphe antarctica*)
N. Bottlenose whale (*Hyperoodon ampullatus*)	Bluespotted stingray (*Neotrygon kuhlii*)
Subantarctic fur seal (*Arctocephalus tropicalis*)	Manta ray (*Manta spp.*)
Australian fur seal (*A. pusillus*)	Tiger shark (*Galeocerdo cuvier*)
New Zealand fur seal (*A. forsteri*)	Great white shark (*Carcharodon carcharias*)
Largha seal (*Phoca largha*)	Grey reef shark (*C. amblyrhynchos*)
Walrus (*Odobenus rosmarus*)	Porbeagle shark (*Lamna nasus*)
Southern sea lion (*Otaria flavescens*)	St Joseph's shark (*Callorhinchus capensis*)
Sea otter (*Enhydra lutris*)	Hammerhead shark (*Sphyrna sp.*)
Imperial shag (*Leucocarbo atriceps*)	Scalloped hammerhead (*Sphyrna lewini*)
Albatross (*Diomedea spp* .)	Green sea turtle (*Chelonia mydas*)
Royal penguin (*Eudyptes schlegeli*)	Pig (*Sus scrofa*)
Macaroni penguins (*E. chrysolophus*)	

Table 4. This table illustrates the preferred diet of each ecotype and the prey species that each group was observed to have eaten. Highlighted in blue are the species which do not align with that ecotype's preference. Only four of the ten groups analysed did not stray from their preferred prey type. These were the Resident, North Atlantic Type I, Gerlache and Subantarctic.

Ecotype	**Transient**	**Resident**	**Offshore**	**NA Type I**	**NA Type II**	**Type A**	**Type B (big)**	**Type B (small)**	**Type C**	**Type D**
Preferred diet	Cetaceans Pinnipeds	Fish Squid	Fish	Fish Pinnipeds	Cetaceans	Cetaceans Pinnipeds	Pinnipeds	Penguins	Fish	Unknown
Observed prey	Minke whale (*Balaenoptera acutorostrata*) Grey whale (*Eschrichtius robustus*) Humpback whale (Megaptera novaeangliae) Bowhead whale (*Balaena mysticetus*) Beluga (*Delphinapterus leucas* Narwhal (*Monodon monoceros* Dall's porpoise (*Phocoenoides dalli*) Harbour porpoise (*Phocoena phocoena*) Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) N. elephant seal (*M. angustirostris*) N. fur seal (*Callorhinus ursinus* Harbour seal (*Phoca vitulina*) Ringed seal (*Pusa hispida*) Harp seal (*Pagophilus groenlandicus*) Bearded seal (*Erignathus barbatus*) Hooded seal (*Crystophora cristata*) Sea lion (*Otariinae sp.*) Steller sea lion (*Eumetopias jubatus*) California sea lion (*Zalophus californianus*) River otter (*Lontra canadensis*) Common murre (*Uria aalge*) White-winged scoter (*Melanitta deglandi*) Cormorant (*Phalacrocoracidae* sp.) Squid (unspecified) Deer (*Cervidae sp.*) Moose (*Alces alces*)	Squid (unspecified) Atka mackerel (*Pluerogrammus monoterygius*) Chinook salmon (*Oncorhynchus tshawytscha*) Chum salmon (*O. keta*) Coho salmon (*O. kisutch*) Sockeye salmon (*O. nerka)* Pink salmon (*O. gorbuscha*) Steelhead salmon (*O. mykiss*) Pacific halibut (*Hippoglossus stenolepis*) Flatfish (*Plueronectiformes sp.*) Sculpin (*Cottoidea sp.*) Pacific herring (C*ulpea pallasii*) Yelloweye rockfish (*Sebastes ruberrimus*) Sablefish/Blackcod (*Anoplopoma fimbria*) Pacific lamprey (*Entosphenus tridentatus*) Lingcod (*Ophiodon elogatus*) Greenling (*Hexagrammidae sp*.)	Fish (unspecified) Salmon (*Salmonidae sp.* Sculpin (*Cottoidea sp.*) Pacific sleeper shark (*Somniosus pacificus*) Leatherback turtle (*Dermochelys coriacea*) Crab (unspecified)	Grey seal (*Halichoerus grypus*) Fish (unspecified) Herring (*Clupea harengus*) Mackeral (*Scrombridae sp.*) Atlantic bluefin tuna (*T. thynnus*) Lumpfish (*Cyclopteridae sp*.)	Baleen whale (unspecified) Harbour porpoise (*P. phocoena*) Fish (unspecified)	Minke whale (*B. bonaerensis*) Dwarf Minke whale (*B. acutorostrata* - subspecies) Sei whale (*B. borealis*) Bottlenose dolphin (*Tursiops truncatus*) Dugong (*Dugong dugon*) S. Elephant seal (*Mirounga leonina*) South American fur seal (*A. australis*) South American sea lion (*Otaria flavescens*) Kelp gull (*Larus dominicanus*) Penguin (unspecified) King penguin (*Aptenodytes patagonicus*) Crested penguin (*Eudyptes spp.*) Gentoo penguin (*Pygoscelis papua*) Chinstrap penguin (*P. antarcticus*) Magellanic penguin (*Spheniscus magellanicu* s) Humboldt penguin (*S. humboldti* Squid (unspecified) Fish (unspecified) Southern hake (*Merluccius australis*) Patagonian toothfish (*Dissostichus eleginoides*) Elasmobranch (unspecified) Leatherback turtle (*Dermochelys coriacea*)	Minke whale (*B. bonaerensis*) Humpback whale (*M. novaeangliae*) Fin whale (*B. physalus*) S. elephant seal (*Mirounga leonina*) Antarctic fur seal (*Arctocephalus gazella*) Weddell seal (*Leptonychotes weddellii*) Crabeater seal (*Lobodon carcinophaga*) Leopard seal (*Hydrurga leptonyx*) Adelie penguin (*Pygoscelis adeliae*) Emperor penguin (*A. forsteri*) Crested penguin (*Eudyptes spp.*) Rockhopper penguin (*E. chrysocome*) Gentoo penguin (*Pygoscelis papua*) Magellanic penguin (*Spheniscus magellanicu* s) Patagonian toothfish (*Dissostichus eleginoides*)	Penguin (unspecified) Gentoo penguin (*Pygoscelis papua*) Chinstrap penguin (*P. antarcticus*)	Humpback whale (*M. novaeangliae*) Emperor penguin (*A. forsteri*) Squid (unspecified) Fish (unspecified) Antarctic toothfish (*D. mawsoni*)	Patagonian toothfish (*Dissostichus eleginoides*)

DISCUSSION

PREY PREFERENCE

This study found prey preferences to be less rigid than previously indicated, with only four of the ten ecotypes not straying from their preferred prey type. The extensive range of prey that the species eat overall was demonstrated, with more prey species being identified than in similar meta-analyses carried out in the past. A study by Jefferson and colleagues (1991) provided a comprehensive summary of all marine mammals that had been observed as killer whale prey up to 1991. The authors state that attacks had been witnessed on 20 species of cetaceans, 14 species of pinnipeds, the sea otter (*Enhydra lutris*, Linnaeus, 1758), and the dugong (*Dugong dugon*, Müller 1776) (Jefferson et al., 1991). This report was the most comprehensive found throughout this review, in terms of global prey preferences; however, it only highlighted killer whale interactions with marine mammals and failed to identify the ecotype or population responsible for the predation events. This limited its usefulness in the ecotype preference analysis. The present study identified 17 cetacean and 10 pinniped prey species, in addition to those highlighted in the paper by Jefferson and colleagues (1991). This could potentially be due to a change in prey distribution or availability, or, alternatively and more probably, it could be as a result of the increased accessibility of information now available.

Northern Hemisphere ecotypes were found to be more restrictive than their Southern Hemisphere counterparts. A report by Barrett-Lennard and Heise (2006) discussed the findings of a study carried out in British Columbia in 1970. This study involved taking three Transient killer whales into captivity to observe their response when fed nothing but salmon (Barrett-Lennard & Heise, 2006). After 75 days of refusing the provided salmon, one of the killer whales died of suspected starvation (Barrett-Lennard & Heise, 2006). The other two orca started eating salmon on the 79th day, but when released back into the wild soon after they immediately returned to their preferred marine mammal prey (Barrett-Lennard & Heise, 2006). This study highlighted the extent to which some groups adhere to their preferences. Interestingly, this report found Transient killer whales to consume quite a broad spectrum of prey, although their preference for marine mammals persisted. Harbour seals were their most common prey type, which matched with the finding of Ford and colleagues (1998), whose study found that 53% of the prey eaten by Transient killer whales were harbour seals, which they attributed to the seals' generally high abundance and relative ease of capture.

A significant exclusion from the prey types eaten by Transient killer whales was salmon, the known preference for their sympatric eastern North Pacific counterparts, Resident killer whales. This stark contrast in the prey eaten by two groups which live in such close proximity highlights the complex nature of the ecotype definition system. While the Northern Hemisphere ecotypes are morphologically similar and often share overlapping territories, the level of distinction between their prey preferences is much more pronounced. A study of harbour seal behaviour carried out by Deecke, Slater and Ford (2002) analysed seal responses when exposed to the underwater vocalisations of both Transient and Resident ecotypes. The harbour seals became agitated and attempted to hide at the surface when presented with the Transient's calls; however, no change in behaviour was observed when played the calls of the Resident's. These responses support the theory that these two groups do not alternate between preferred prey types.

A report by Springer and colleagues (2003) discussed the potential impact that industrial whaling had on influencing predation targets of killer whales. The industrial whaling period decimated many of the once abundant whale species across most of the world's oceans. The authors suggested that this could have led to the northern mammal eating killer whale populations switching their larger cetacean prey preference to pinnipeds and sea otters in response to the reduced prey availability (Springer et al., 2003). This argument has been disputed in studies by Mizroach and Rice (2006) and Mehta and colleagues (2007), who state that there is insufficient evidence to suggest Transient killer whales ever relied heavily on large cetacean species as prey in the eastern North Pacific Ocean.

Some of the Southern Hemisphere ecotypes displayed more generalist tendencies. Two of these ecotypes, the Gerlache and the Subantarctic, were found to predate only on their preferred prey types; however, unlike those found in the Northern Hemisphere, these two groups were only represented by six reports in total. This made drawing conclusion from their data particularly difficult and highlighted just one of the challenges faced with analysing killer whale ecology, i.e. sampling bias. A study by Pitman and Ensor (2003) discussed the dietary specialisations of Southern Ocean killer whales, Types A, B, and C. They discuss the findings of the Soviet whaling period in 1979/80, which analysed the stomach contents of 785 killer whales harvested over the summer period (Berzin & Vladimirov, 1983; Pitman & Ensor, 2003). The Soviet fleet classed the two types of orca caught as two different species, identifying them as *O. orca* and *O. glacialis*, or 'white' and 'yellow' respectively (Berzin & Vladimirov, 1983; Pitman & Ensor, 2003). Today these classifications are not recognised, however, they are thought to be in reference to the Antarctic (Type A) and Ross Sea (Type C) ecotypes due to their descriptions and stomach contents, although this cannot be confirmed (Pitman & Ensor, 2003). Stomach contents indicated that *O. orca* predated on mostly marine mammals (89.7%), followed by squid (7.1%) and fish (3.2%). *O. glacialis* was found to consume mainly fish (98.5%), with extremely low quantities of squid (1.1%) and marine mammals (0.4%) (Berzin & Vladimirov, 1983).

A study by Pitman and Durban (2011) found Pack Ice killer whales to demonstrate a much greater affinity for predating on Weddell seals (*Leptonychotes weddellii*, Lesson 1826) than any other pinniped species. The study found that when the killer whales encountered Weddell seals, they attacked 94% of the time (16/17), however, only attacked crabeater and leopard seals in 14% of interactions, often abandoning the pursuit (Pitman & Durban, 2011). The behaviour of the killer whales was interpreted by the authors to be hesitant when pursuing both crabeater and leopard seals, and after inspecting the seals more closely they were often left behind unharmed (Pitman & Durban, 2011). Those findings differed markedly from those in this study, which identified crabeater seals as the most common prey for this ecotype.

Pitman and Durban (2010) also commented on the energy benefit of Gerlache (Type B, small) killer whales feeding on penguins, which are, in relation to the killer whale size, very small. The species of penguins observed being eaten in their study, chinstrap, gentoo and Adelie (*Pygoscelis adeliae*, Hombron & Jacquinot 1841), have a mean body mass of between 4–6 kg, less than 0.2% of the mass of an adult female killer whale, which can weigh over 3000kg (Pitman & Durban, 2010). It is uncertain what benefits are gained by eating such small prey, particularly if they only eat certain parts. The efficiency of the hunt, i.e. the energy expelled while chasing them and processing them, has a significant impact on the benefits provided (Pitman & Durban, 2010). During one of the observations of the study, which lasted 3.6 hours, one group of six killer whales successfully hunted at least five penguins and chased, but lost, at least four more, with each attempt lasting for less than 2 minutes (Pitman & Durban, 2010). This is a significantly shorter hunting time than those that involve much larger prey. A study by Ford and colleagues (2005) discussed the predation tactics adopted by Transient killer whales when hunting minke whales. The report highlighted the significant amount of time that the pods spend chasing their prey, often lasting a number of hours, resulting in a much higher energy output but providing a significantly more substantial prize (Ford et al., 2005).

BEYOND PREY PREFERENCE – PART PREFERENCE

Some killer whale populations display even more particular predation habits, eating only a portion of their kill (Ferguson et al., 2012). As highlighted by reports of predation on great white sharks (*Carcharodon Carcharias*, Linnaeus 1758), sting rays, and some Southern Ocean penguin and seal species, some killer whale types move beyond simple prey preference, and eat only certain parts of their prey (Fertl, Acevedo-Gutierrez & Darby, 1996; Morrice, 2004; Visser, 2005; Pitman & Durban, 2010; Ferguson et al., 2012; Kock & Engelbrecht, 2019). While hunting penguins, Gerlache killer whales reportedly showed a noticeable preference for only the breast meat, or pectoral girdle, of their prey, and displayed extreme care when dismembering the carcasses (Figure 14) (Pitman & Durban, 2010). This was noted on most occasions where remains were left floating on the surface, although on some occasions no remains could be found at all, which led to the assumption that the birds are sometimes swallowed whole (Pitman & Durban, 2010).

'Wasteful behaviour' was also witnessed in the Antarctic Peninsula area where Pack Ice killer whales were seen feeding on Weddell seals (Pitman & Durban, 2011). In the study by Pitman and

Durban (2011), the authors highlight a single occurrence where an estimated 45kg of Weddell seal remains were left on the surface after a kill. This was different to the other recorded attacks in the area, after which only small scraps of the prey were seen at the surface (Pitman & Durban, 2011). This event supported the hypothesis that some killer whales carefully dismember their prey in order to eat their preferred parts. It was reported that the remains were in particularly good condition, with evidence suggesting members of the group worked together to carefully remove the skin and blubber from the lower part of the body, allowing the body to slide out of the skin in one piece (Pitman & Durban, 2011). The paper highlights the fact that the population observed in this study appeared to be extremely well fed which is considered to be an influencing factor of prey part specialisation. The authors state that "an adult male… was the fattest killer whale we have ever seen in the wild" (Pitman & Durban, 2011). However, evidence also suggested that there are times when Pack Ice killer whales are less selective. The paper by Pitman and Durban (2011) also highlighted the historical events of killer whales consuming only the lips and tongues of whales killed during whaling operations and grey whale calves that died during the migration to higher latitudes.

Figure 14. Remains of chinstrap penguin found on surface after attack by small Type B killer whales in the Gerlache Strait. Remains indicate that only the pectoral crest was taken, i.e. the breast meat, while the rest of the animal was discarded. (Image taken from Pitman & Durban, 2010, Original source: E. White.)

Elasmobranch specialists also appear to share this trait, with many reports indicating the liver is the target organ (Fertl, Acevedo-Gutierrez & Darby, 1996; Morrice, 2004; Visser, 2005; Kock & Engelbrecht, 2019). Reports of this behaviour indicated the same specialised trait, with much of the carcass left untouched, excluding the section of abdomen containing the liver. A study by Reyes and Garcia-Borboroglu (2004) discussed the observations of researchers off the coast of Patagonia, where 17 sevengill sharks (*Notorynchus cepedianus*, Péron 1807) were found washed up on shore, many of which appeared unharmed and were thought to have deliberately beached themselves to escape predation. Others had distinct killer whale bite marks and were missing a part of their abdomen containing the liver (Reyes and Garcia-Borboroglu, 2004). In 2015, several sevengill sharks were found dead by scuba divers in the Table Mountain National Park marine protected area (MPA) (Kock & Engelbrecht, 2019). Following the discovery of more dead sharks in the months after, these deaths were eventually linked to an increase in killer whale sightings in the region (Kock & Engelbrecht, 2019). Between 2015 and 2017, the same two male killer whales were seen near the site of these predation events and are also suspected to be responsible for the death of five great white sharks in Gansbaai, South Africa (Kock & Engelbrecht, 2019). All these reports highlighted a similar wound pattern between their pectoral fins and a missing liver, while the other internal organs remained untouched (Kock & Engelbrecht, 2019). The wound patterns indicate the pectoral fins were pulled apart in order to open the body cavity, allowing for the removal of the liver (Kock & Engelbrecht, 2019). A shark's liver is rich in fat and contributes up to a third of its total body weight (Kock & Engelbrecht, 2019), potentially explaining why this specialist behaviour has been witnessed in regions across the world.

Inuit hunters also reported on the prevalence of prey wastage in the Nunavut territory of Canada (Ferguson et al., 2012). Eleven interviewees across four different communities reported events where beluga (*Delphinapterus leucas*; Pallas 1776), narwhal (*Monodon monoceros*, Linnaeus 1758), and bowhead whales (*Balaena mysticetus*, Linnaeus 1758) had been killed with only a small portion of meat being eaten (Ferguson et al., 2012). This behaviour was disparaged by five of the interviewees, due to the wasted food; however, three commented positively saying they could collect *maqtaq*, or whale skin and blubber, from the remains of the abandoned whale carcasses (Ferguson et al., 2012).

CONSERVATION IMPLICATIONS OF PREY SPECIALISATION

Due to their dwindling population numbers, Southern Resident killer whales are currently listed as 'endangered' on the Endangered Species Act and 'depleted' under the Marine Mammal Protection Act (MMC, n.d.). That population currently consists of three pods, represented by a total of 75 individuals (Ayres et al., 2012). The decrease has been correlated with a variety of factors, including pollution, increasing boat traffic, and a significant decrease in their preferred prey species, chinook salmon (Erbe, 2002; Williams, Trites & Bain, 2002; Ford, Ellis & Olesiuk, 2005; Ayres et al., 2012; Foster et al., 2012). Chinook and chum salmon are the main species that this group has been recorded eating, which is correlated with their relatively high fat content, when compared to the other smaller salmon species available (Erbe, 2002). Reports also indicate that chinook salmon may be the least abundant species within the Resident's range, indicating the significant threat posed by a too stringent prey preference (Ford et al., 2005). Residents were found to predate on six different salmon species, though to varying levels, and overall have been recorded eating 16 species of fish. Chinook was their most significant prey source, a widely accepted theory in the literature reviewed (Ford et al., 1998; Ayres et al., 2012). A study by Ford and colleagues (1998) highlighted the significant preference that Resident killer whales display for chinook salmon in the eastern North Pacific. The study spanned a 20-year period and was the first comprehensive look at the differences between Transient and Resident killer whales (Ford et al., 1998). From analysis of stomach contents and field observations, chinook salmon was found to represent 65% of the total prey eaten by Resident killer whales (Ford et al., 1998). The report also discusses the occurrence of Resident's 'harassing' marine mammals, though none have ever been recorded in their stomach contents (Ford et al., 1998). The study found Transients to have a more generalist diet, although they still showed a strong preference for marine mammals, particularly pinnipeds (Ford et al., 1998).

The potential threat posed to the Ross Sea (Type C) killer whales by the Southern Ocean's growing Antarctic toothfish fishery played an influential role in the designation of the Ross Sea MPA (Ainley, Ballard & Olmastroni, 2009; Ainley & Ballard, 2012). A study by Ainley and colleagues (2009) discussed the apparent decrease of Ross Sea (Type C) killer whales within their home range. The authors suggested that the change in range for this ecotype could be driven by "an industrial fishery-driven, density-dependant northward contraction of the toothfish stock". This parallels the response of the Northern Hemisphere's Resident killer whales, which decreased in abundance following a reduction in their larger preferred prey type (Ainley et al., 2009).

Another aspect of conservation that needs to be considered is the impact that these 'wolves of the sea' could have on other species (Springer et al., 2003). Reports have highlighted the potential for killer whales significantly reducing the abundance of narwhals and belugas (Ferguson et al., 2012; Laforest, 2015). A significant population of belugas migrate to Hudson Bay in the Canadian Arctic every summer (Laforest, 2015). Previous reports indicate that orcas were not known to be present in that region prior to the 1950s, however, there has been an increase in the number of reported sightings (Laforest, 2015). As beluga are a significant orca prey source, an increase in killer whale abundances within this important feeding and breeding ground could have detrimental impacts on beluga abundance. The paper by Springer and colleagues (2003), which discussed the potential for killer whale diets to have changed in response to industrial whaling, was motivated by the noticeable population decreases of Steller sea lions and sea otters in the areas where Transient killer whales roam. While the claims made in their paper made have been disputed by others (Mizroach & Rice, 2006; Mehta et al., 2007), the fact that killer whales hold significant influence over the abundance and stability of their prey species populations is a widely accepted theory (Guinet et al., 1992; Estes et al., 1998). Killer whales are also credited with influencing the migratory breeding behaviour of high latitude whale species due to the threat of predation that they pose to their calves (Guinet et al., 1992; Estes et al., 1998; Pitman & Durban, 2011). There is currently not enough known about killer whale feeding habits in every ecosystem to infer the potential impact they may have on the structure of their marine communities.

A study by Pitman and Durban (2010) suggested that killer whales may have been responsible for the 50% decline in emperor penguin (*Aptenodytes forsteri*, Gray 1844) abundance in Adelie Land in the late 1970s. A Soviet research expedition took place in the region and analysis of the stomach contents of the 444 killer whales killed during that period failed to find any identifiable penguin remains (Pitman & Durban, 2010). However, the hunting methods often adopted by penguin-eating killer whales and their perceived preference for breast meat, which, due to lack of bones, shows no significant penguin characteristics, the potential that killer whales were responsible for the dramatic decrease in population could not be ruled out (Pitman & Durban, 2010). This correlates with the previously discussed phenomenon of part preference and, as highlighted by Pitman and Durban (2011), this could mean that a higher number of individuals are needed to be killed to gain enough energy for their metabolic needs. This indicates a greater need to understand the prevalence of part preference predation, in order to infer the potential implications for the prey species populations.

The increasing occurrence of killer whales depredating fish off longlines also poses a significant conservation risk (Dalla Rosa & Secchi, 2007; Hamer, Childerhouse & Gales, 2012; Tixier, Garcia, Gasco, Duhamel & Guinet, 2015; Werner, Northridge, Press & Young, 2015; Lennert & Richard, 2017). This study found 55 occasions where depredation had occurred, these reports spanned a variety of fish species. The risk of killer whales being killed as bycatch is a concern, however, the more common hazard is retaliation by upset fishers (Hamer et al., 2012; Tixier et al., 2012; Werner et al., 2015; Lennert & Richard, 2017). A study by Visser (2000) discussed the growing reliance that some killer whale populations have on longline fisheries. The report highlighted a stranding event that occurred on the West Coast of New Zealand's North Island in 1991, where a female killer whale was found with marks consistent with those found on cetaceans that had been bycaught in fishing net or line. This individual also had five wounds that were thought to be either bullet holes or from being hit with a sharp object. In the same report, Visser (2000) also reports on the killer whale that was hooked in the back by a Japanese tuna longlining vessel off the Bay of Plenty in 1990. On this occasion, the orca was hauled alongside the boat, allowing itself to be cut free and released alive, but this event highlights the potential for less fortunate outcomes (Visser, 2000).

Killer whales are extremely intelligent and socially complex creatures that have been shown to pass learnt traits down through their generations (Visser, 2000). The growing understanding that by following fishing vessels they will get access to an easy meal has been displayed through the increasing prevalence of this behaviour worldwide (Hamer et al., 2012; Tixier et al., 2012; Werner et al., 2015). Killer whales often appear as the fishing vessels begin to haul the gear in, potentially attracted by the sound of gear being hauled and associating that sound with an opportunity to feed (Visser, 2000). There have also been a number of firsthand reports of fishers witnessing killer whales teaching their young how to take fish off lines; the report by Visser (2000) discusses the event where an orca calf was seen eating a bluenose off a longline and then suckling from its mother shortly thereafter, highlighting the young age at which individuals are taught this depredation behaviour.

A range of methods, including acoustic and physical mitigation methods, have been attempted to reduce the prevalence of orca depredation, however, few have found to be effective (Hamer et al., 2012; Tixier et al., 2012; Werner et al., 2015). Acoustic mitigation technologies have been trialled, though were found to be insufficiently developed and their effectiveness was unable to be assessed (Hamer et al., 2012). Killer whales were also been reported to associate the acoustics, supposedly aimed to repel them, with a 'dinner-bell' effect, being more attracted to boats after the alarm was sounded (J. Fenaughty, pers. comm.). Physical mitigation methods required more complex equipment though these were generally easier to develop (Hamer et al., 2012). Adequate reductions in the risk of marine mammal bycatch will require significant further development of these technologies.

CRITICISM AND LIMITATIONS

SAMPLING BIAS

Sampling bias provides a substantial challenge when attempting to analyse the ecology of killer whales globally, but particularly for the Southern Hemisphere populations. The Southern Hemisphere ecotypes are significantly more isolated than their northern counterparts, with much of their range being open ocean or the Antarctic coast, which have very few visitors in comparison to the land surrounding the northern ecotype's range. Two of the Southern Ocean ecotypes, Gerlache (Type B, small) and Subantarctic (Type D) were found to only predate on their preferred prey, penguins and fish, respectively; however, there was only six reports in total for both groups combined. The likelihood of finding an outlier with such limited data is very slim, particularly when the perceived preferences are based on what these groups have been observed eating. These two ecotypes could potentially be as restrictive as the Northern Hemisphere's Resident killer whales, but that conclusion could not be drawn from this data set.

Sampling bias is also a challenge when identifying seasonal prey switching of ecotypes. Ford and colleagues (1998) commented on the limitation that exists within the seasonality of the higher latitudes and the lack of available information regarding killer whale behaviour over the winter months, producing incomplete data sets. The wet season in the lower latitudes (Dec–Feb) also has potential to produce observer bias, where there are fewer boats on the water to see the orca, so in turn, some assume they are absent (Visser & Bonaccorso, 2003). Sampling of the Southern Ocean in the austral winter is extremely limited (Pitman & Ensor, 2003). Many of the ecotypes are known to leave Antarctica during this time, migrating to more temperate waters of the lower latitudes. Antarctic (Type A) killer whales have yet to be seen in Antarctic waters during the austral winter months, often following their preferred minke whale prey north and spending the winter months hunting a wider variety of prey in the waters surrounding South America, Australia, and New Zealand (Pitman & Ensor, 2003; de Bruyn et al., 2012). Records have shown that Pack Ice (Type B, large) and Ross Sea (Type C) killer whales often remain in the Antarctic region for part of the winter, though individuals with their distinctive caped pattern have been seen as far north as Tahiti in March 2001, indicating a tropical migratory behaviour (Pitman & Ensor, 2003).

LACK OF ECOTYPIC IDENTIFICATION

Of the 178 prey types identified, reports involving 61 of those did not identify the associated ecotype that was responsible to the predation event. This meant that the data was unable to be used in understanding whether that event was in line with the perceived preference for that population.

Papers by Wellard and colleagues (2016) and Samarra and colleagues (2018) discussed the predation behaviour of the North Atlantic populations; however, they diverted from the known ecotype definitions, North Atlantic Type I and Type II. These two papers separated the populations further into three groups: Populations A, B, and C (Wellard et al., 2016; Samarra et al., 2018). These new classifications meant that their valuable data was unable to be used in analysis because it became unclear which population correlated with which ecotype and therefore, which population was perceived to prefer which prey. The study by Samarra and colleagues (2018) stated that a genetic study was carried out which indicated the presence of three genetically distinct populations which is why they adopted that classification method rather than the widely recognised ecotypes.

ACCURACY OF PREY IDENTIFICATION

In a study such as this, accurate identification of prey species is a crucial component. Some papers only provide general overviews of prey type, such as "baleen whale", "marine mammal" or "fish", rather than specifying the species (de Bruyn et al., 2012; Wellard et al., 2016; Capella et al., 2014). The decision was made to keep this data in the analysis, as it was beneficial in highlighting the types and range of prey eaten, particularly those that lie outside the expected preferences; however, this information was excluded from the prey species totals. Another challenge faced was discrepancies between the common names used for species. Blue-eye trevalla and Deepsea trevalla were identified as two species of prey eaten by killer whales in the waters surrounding New Zealand and Australia (Visser, 2000; Morrice, 2004; Tixier et al., 2018). In the final stages of analysis, these reports were found to represent the same species, *Hyperoglyphe antarctica*. This highlighted a limitation introduced by inexperience of the author, the importance of accurate scientific nomenclature early in analysis, and introduces some uncertainty surrounding the high number of species previously reported on.

RELIABILITY OF DATA

The reliability of the data varied considerably. Some reports provided reliable first-hand accounts of predation events, where the chase, kill and consumption of the prey species was recorded in precise detail (Visser, 2000; 2005; Visser, Berghan, van Meurs & Fertl, 2005; Visser et al., 2008;

2010). Others used interviews, such as the report by Ferguson and colleagues (2012) which reported on the predation habits of killer whales in Nunavut, Canada, through talking with Inuit hunters. This report provided great insight into the predation behaviour of killer whales in the region, although some statements were second-hand which brings into question the reliability of some statements reported (Ferguson et al., 2012). When discussing the prevalence of the fish predation in the area, seven interviews reported that killer whales did eat fish, though none of them had witnessed it themselves (Ferguson et al., 2012). The report provided adequate mitigation for the question surrounding reliability the stories, identifying separate reports of first- and second-hand accounts (Ferguson et al., 2012).

Another challenge discussed by Ford and colleagues (1998) was the margin for error that exists around secondary prey remains. Analysis of stomach contents is thought to provide a clear picture of the species that that individual had eaten. However, it is possible for a species to be found in a killer whale stomach due to being eaten by another species that had also been predated on. A squid beak was found in the stomach of a stranded Transient killer whale in Vancouver Island, eastern North Pacific (Ford et al., 1998). This species was recorded as prey for the ecotype, however, the authors stated that it was unclear whether the squid had been consumed by the orca or was eaten by the Northern elephant seal (*M. angustirostris*, Gill 1866), whose remains were also present in the same stomach (Ford et al., 1998).

A report by Pitman and Ensor (2003) highlights the challenges faced with interpreting the harassment behaviour that is present in most killer whale societies. The data in the current report indicates that Ross Sea (Type C) killer whales were also seen to ‘predate’ upon humpback whales, which is a considerable diversion from the perceived fish preference. Pitman and Ensor (2003) include a report from 6 January 1981 from Payne and Crawford (1989) in their analysis which states five subgroups of Type C killer whales were seen possibly attacking a pod of humpback whales. The lack of conclusive evidence surrounding this event meant that confirming that predation actually occurred is impossible, and therefore, this species should be excluded from the prey species identified for this group.

PREVALENCE OF LETHAL HARASSMENT & SURPLUS KILLING

The prevalence of lethal harassment and surplus killing also highlighted the question of reliability in some reports, where it was difficult to distinguish between events of these types and an actual predation event (Williams, Dyer, Randall, & Komen, 1990; Ford et al., 1998; Pitman & Durban, 2010; Ferguson et al., 2012). The study by Ford and colleagues (1998) adopted a thorough definition of observed predation events, where visual or physical evidence was provided that indicated the prey species had been killed and consumed. Evidence included prey being held in a killer whale’s mouth and blood or remains being seen in the water (Ford et al., 1998). ‘Harassment’ was assigned when pursuit or predatory interactions occur, but no kill could be confirmed (Ford et al., 1998). While thorough, there is still potential for misinterpretations to occur, especially as very little of the interactions happen on the surface and visibility underwater is limited (Ford et al., 1998).

The study by Ferguson and colleagues (2012) reported on the recollections of eight Inuit hunters which state that killer whales are thought to ‘kill for fun’ on occasion, killing without consuming their prey or ‘playing’ with other wildlife, resulting in its death. An interviewee also discussed an event where killer whales were responsible for killing “hundreds” of belugas and not eating them at all (Ferguson et al., 2012). This interviewee said that once the killer whales had departed, Inuit arrived and collected *maqtaq* from a number of the dead, but largely intact, beluga (Ferguson et al., 2012).

Another report by Barrett-Lennard and Heise (2006) also highlights the prevalence of surplus killing and lethal harassment. The authors discuss an event where two killer whales were responsible for killing more than 290 cormorants over a four-day period, none of which were eaten (Barrett-Lennard & Heise, 2006), highlighting the impact that killer whales can have on species abundances across many trophic levels.

CONCLUSIVENESS OF RESULTS

The literature search was as thorough as possible given the time restraints set for this project; however, the conclusiveness of the results was limited given the array of information that is still available for review. While an extensive list of prey species was identified through this study, due to new species being continually added, even while the data analysis and report writing had commenced, a data collection endpoint was selected to allow for the information already gathered to be accurately analysed. Technological advances have meant that there is a greater volume of information now readily available for relative ease, making the data gathering process in this study much more straightforward than in studies such as Jefferson and colleague's (1991) report. If more time is made available, and resources are provided to carry out surveys of the vocal marine science community, there is certainty that more species will be identified as killer whale prey. There is also potential to provide the database as an opensource resource allowing for information to be continually added, increasing the scope of the study and, in turn, increasing the understanding the roles of killer whales in ecosystems around the world.

CONCLUSION

The Oxford dictionary defines preference as 'a greater liking for one alternative over another or others' (Oxford English dictionary, n.d.), which is a significant statement when considering the flexibility of diet witnessed through many of the killer whale populations globally. With only four ecotypes adhering strictly to their preferred diets, and some of those being attributed to a lack of data, it can be concluded that there is more flexibility in many of their diets than previously acknowledged. In a report by Samarra and colleagues (2018), which looked at prey preferences in Icelandic killer whales, it was stated that just because a population may be better adapted at hunting a certain prey, it does not mean they will not stray from it. Preference merely means that, if provided with a range of choices, one will often be chosen over the other.

Prey preference has been found to be a highly subjective assignation. Killer whales were found to predate on 159 different prey species, indicating an overall generalist diet. A more reliable indicator of preference would be the prey that are available to the populations which they choose not to predate on. The Transient and Resident killer whales, which live sympatrically, have very different prey preferences, and have never been recorded eating the primary prey source of the other. The Southern Ocean ecotypes, however, have been found to eat many of the species available to them, with some of the groups showing extensive generalist behaviour, as well as seasonal prey-switching.

An important theory illustated by this study is that the overall distinction between the different groups of orcas globally is extremely complex and each population does not easily fit into distinct classifications. Other than the ten recognised ecotypes, there are numerous other populations around the world which differ in their own ways, such as the New Zealand population, which specialise in elasmobranchs but have been observed hunting cetaceans (Constantine, Visser, Buurman & McFadden, 1998), and the Marion Island population, which shares similar morphological traits to both Type A and Type B killer whales and eats a variety of prey including marine mammals, penguins, and fish (Condy, van Aarde & Bester, 1978; Reisinger et al., 2011).

The conclusions drawn in the study by de Bruyn and colleagues (2012) are similar to those drawn here. The Southern Hemisphere ecotypes are not as distinct as their northern counterparts and the premature assignation of ecotype status could have detrimental effects when the assumptions made about their role in the ecosystem are based on those in the Northern Hemisphere (de Bruyn et al., 2012). A greater understanding of the abundances and feeding habits of each ecotype is required to provide an accurate insight into the impact that these apex predators can have on their ecosystems, and the impact that changes in their ecosystems could have on them.

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APPENDICES

Appendix A.

An example of the Microsoft Excel spreadsheet where the data was collated. The columns are

i) Prey type
ii) Location
iii) Ecotype/population
iv) Source
v) Original source cited by paper and/or any extra information provided

N. Elephant Seal	Vancouver Is., ENP	Transient	Ford et al., 1998	Baird & Dill, 1995
	Vancouver Is., ENP	Transient	Ford et al., 1998	*found in stomach of stranded orca
	Northern Hemisphere	No ID	Jefferson et al., 1991	*3 predatory events, 0 non-predatory events
S. Elephant Seal	MacQuarie Is., Subantarctic	No ID	Travers et al., 2018	
	Marion Is., Subantarctic	A (Antarctic)	de Bruyn, Tosh, Terauds, 2012	Condy et al., 1978
	Marion Is., Subantarctic	B (Pack ice)	de Bruyn, Tosh, Terauds, 2013	Condy et al., 1979
	MacQuarie Is., Subantarctic	A (Antarctic)	de Bruyn, Tosh, Terauds, 2012	Morrice, 2004
	Southern ocean	B (Pack ice)	Pitman & Ensor, 2003	Pitman pers obv.
	Antarctica	B (Pack ice)	Pitman & Durban, 2011	Pitman & Ensor, 2003, Visser et al., 2008, Ainley et al., 2009
	Antarctic Peninsula	B (Pack ice)	Pitman & Durban, 2011	
	Crozet Is., Subantarctic	A (Antarctic)	Pitman et al., 2010	Guinet 1992, Guinet et al., 2000
	Subantarctic Islands	A (Antarctic)	Capella et al., 2014	Guinet et al. 2000; 2007 *resemble type A
	Southern Hemisphere	No ID	Jefferson et al., 1991	*250+ predatory events, 0 non-predatory events
	Southern Africa	No ID	Best, Meyer & Lockyer, 2010	*vibrissae and nails
	Marion Is., Subantarctic	No ID	Reisinger et al., 2011	*killed and eaten on two occasions
	Northern Patagonia	No ID	Reisinger et al., 2011	Iniguez et al., 2002 *3.9%
Fur seal	New South Wales, Australia	No ID	Morrice, 2004	
	Tasmania, Australia	No ID	Morrice, 2004	
	Victoria, Australia	No ID	Morrice, 2004	
Antarctic Fur seal	MacQuarie Is., Subantarctic	No ID	Travers et al., 2018	
	Marion Is., Subantarctic	A/B	de Bruyn, Tosh, Terauds, 2012	Reisinger et al., 2011c
	Antarctic Peninsula	B (Pack ice)	Pitman & Durban, 2011	Dalla Rosa et al., 2007 *unconfirmed
	MacQuarie Is., Subantarctic	No ID	Morrice, 2004	
Subantarctic Fur seal	Marion Is., Subantarctic	No ID	Reisinger et al., 2011	*all pups, killed and eaten x3
N. Fur seal	Far Eastern Russia	No ID	de Bruyn, Tosh, Terauds, 2012	Burdin et al., 2007
	Aleutian Islands, Alaska	Transient	Matkin et al., 2007	
	Northern Hemisphere	No ID	Jefferson et al., 1991	*3+ predatory events, 0 non-predatory events
Australian Fur seal	Southern Australia	No ID	Morrice, 2004	
	MacQuarie Is., Subantarctic	No ID	Morrice, 2004	
NZ Fur seal	Southern Australia	No ID	Morrice, 2004	
	MacQuarie Is., Subantarctic	No ID	Morrice, 2004	
South American Fur seal	Chilean Patagonian fjords	A (Antarctic)	Capella et al., 2014	
	Southern Chile	No ID	Capella et al., 2014	Capella et al. 1999; Hucke-Gaete et al. 2004; Häussermann et al. 2013
Grey seal	Iceland	NA Type I	de Bruyn, Tosh, Terauds, 2012	
	Northern British Isles	NA Type I	de Bruyn, Tosh, Terauds, 2012	
	Iceland	NA (not defined)	Samarra et al., 2018	*stranded whale found with pieces of 5 seals in stomach
	Northern Hemisphere	No ID	Jefferson et al., 1991	*3+ predatory events, 0 non-predatory events
	Norway	NA (not defined)	Jourdain et al., 2017	
Largha seals	Far Eastern Russia	No ID	de Bruyn, Tosh, Terauds, 2012	Burdin et al., 2007
Harbour seal	Prince William Sound, Alaska	Transient	Heise et al., 2003	